6 *New approaches to the quantitative analysis of craniofacial growth and variation*

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Why compare growth allometry amongst human populations?

In this chapter we outline some recent developments in the analysis of morphological variation. The focus is on the human facial skeleton but the methods and approaches described can be applied to any situation in which variations in form are to be studied. In particular this chapter presents an account of some recent developments in statistical and graphical approaches to the study of landmark data. Collectively the class of methods that we will use forms a part of the toolkit of 'geometric morphometrics' (Marcus *et al.* 1996).

In order to focus our description of the implementation of geometric morphometric techniques it is illustrated by an example study in which morphological variation is examined between the faces of two groups of people: Aleutians and Alaskans (Inupiaq Eskimos). This study aims to assess the degree and nature of any differences in cranial morphology between adults and to investigate the extent to which such differences can be attributed to differences in patterns of cranial growth.

The example study illustrates an approach that might be applied more widely. Many fossil crania are known and much discussion of human origins hinges on this material. If, however, crania are to form a focus of studies of human evolution and variation in the past then it is important that adult morphology is interpreted from a developmental perspective. This is because adult morphology arises through developmental processes and, in consequence, variations between crania arise through variations in these processes. This leads us to seek an understanding of differences amongst adults in terms of differences in ontogeny in the expectation that adaptive and evolutionary transformations might, in turn, be understood in terms of pattern and process.

Differences between distinct populations might arise simply through truncation or extension (in time or rate; Shea 1983, 1986) of a common

growth pattern. Alternatively differences might be due to the evolution of distinctive patterns of growth. Such distinctiveness might be a feature of the whole of the growth period or it may be confined to one stage of growth. A further possibility is that differences in early development lead to the early establishment of morphological distinctiveness and that this persists into adulthood despite common growth patterns. It is also possible that some combination of differences in early developmental patterning, growth patterning, growth timing and growth rate accounts for differences between adult forms. Knowledge of ontogeny can be expected to provide insights into variation and adaptation through unravelling of the morphogenetic basis of evolutionary adaptation.

Cranial growth

The craniofacial skeleton is made up of distinct skeletal elements. Each develops and grows under the influence of diverse local and systemic factors. Many individual bones can, in turn, be divided into subunits, each of which is potentially subject to different influences during growth. Despite this, the cranium remains a functional whole during growth, and this is achieved through co-ordinated growth and remodelling of individual bones.

Parts of the cranium develop through ossification of cartilaginous models. Three pairs of cartilages contribute to the cranial base: the prechordal and hypophyseal cartilages, mainly derived from the neural crest; and the parachordal cartilages, derived from the occipital sclerotomes and the first cervical sclerotome (Sperber 1989). Endochondral ossification is preceded by hyaline cartilage prototype models of the future bone and is characteristic of the bones of the cranial base. In contrast, intramembranous ossification is characteristic of the bones in the cranial vault, most of the facial bones and the mandible. It takes place in tissues of neural crest origin that form sheet-like osteogenic membranes (Sperber 1989; Moore and Persaud 1993). Sometimes secondary cartilage will appear and later ossify endochondrally in membranous bones, such as the mandible.

Growth involves not only increases in size of the individual elements of the cranium during development but also changes in the spatial relationships and shapes of those elements (Enlow 1975). In humans and mammals generally, growth contributes significantly to final adult morphology, since the craniofacial skeleton undergoes changes in shape as well as size. Thus adult human crania differ considerably in form from those of neonates

because different parts of the skull enlarge at different rates and in different directions. In this chapter we use the term growth allometry to refer to the changes in shape consequent upon differential growth.

Craniofacial skeletal growth consists of three principal processes: conversions of cartilage to bone, sutural deposition and periosteal remodelling (Thilander 1995). The postnatal conversions of cartilage at the cranial base are largely confined to the spheno-occipital synchondrosis, which persists into the late teens, or early adulthood. Although this synchondrosis allows for some linear growth in the cranial base, its most important function is thought to be to adjust the flexure of the cranial base (Thilander 1995). The nasal septum appears (Moss 1964) to grow secondary to displacement of the midfacial bones. It is not, as previously thought, an active participator in the displacement of the midfacial bones during development (Scott 1953, 1956). Bone deposited at sutural edges contributes to growth allometry in that differential deposition at sutures with different spatial orientations results in transformation of cranial form. Sutural deposition is presently thought to occur in response to mechanical stimuli in the sutural membranes (Enlow and Hans 1996).

Growth of cartilages and deposition at sutures leads to the relative displacement of skeletal elements during growth. Functional alignment is maintained in part through co-ordination of these processes and in part through remodelling of existing bone. Bone remodelling is directed towards coordinated resorption and formation. It is regulated by systemic factors such as hormones that control osteoblastic and osteoclastic activity and by the local mechanical, hormonal and vascular environment. Remodelling of the bone surface contributes, together with sutural growth, to the normal development of the sizes and shapes of the bones of the face and vault. This ontogenetic remodelling process is termed 'bone growth remodelling' (Bromage 1986). It is a process that acts to a large extent as a compensatory mechanism, maintaining proper bone alignment, function and proportionate growth during bone displacement (Enlow 1975). The surface distribution of bone growth remodelling processes is therefore considered to be an important indicator of craniofacial growth as a whole (Enlow 1975; Bromage 1986). It is currently hypothesised that growth remodelling acts as a compensatory mechanism to maintain proper bone alignment during displacement (Enlow 1968, 1975). Consequently it has been suggested that the spatial distribution, direction and rate of surface remodelling activity should serve as an indication of the pattern of displacement (Enlow 1975; Bromage 1986).

Cartilaginous growth, sutural deposition and cortical remodelling are regulated and coordinated to ensure functional integrity during cranial

growth. Each region of the skull is subject to its own particular mix of genetic and epigenetic influences during growth and the way in which these are regulated is not fully understood. Moss and his colleagues (Moss 1964; Moss and Salentijn 1969a,b) have proposed a widely accepted model of regulation through 'functional matrices'. Under this model the growth of the skeletal elements is considered secondary to, and guided by, the growth of the functional matrices. These matrices are considered to be of two basic types: periosteal and capsular. Periosteal matrices are ones in which growth is influenced by local effects such as the forces generated by muscles acting on the skeleton through the periosteum. Capsular matrices are ones in which skeletal elements forming a capsule are influenced by their contents.

The neurocranium has thus been considered a capsular functional matrix (Moss and Salentijn 1969a; McLachlan 1994) containing the brain, the leptomeninges and the cerebrospinal fluid. The expanding brain displaces the bones of the neurocranium outward, causing tension in the sutural membranes which in turn respond by depositing bone at the sutural edges (Enlow and Hans 1996). The brain develops very rapidly in early childhood, especially in the first year but its growth is completed long before most other parts of the human body. Thus the neurocranium follows a similar growth course, although the spheno-occipital synchondrosis will keep growing into adulthood to accommodate the posterior expansion of the maxilla as space is made for the molars and growing nasopharynx. Once neurocranial expansion slows down, sutural growth becomes negligible and remodelling becomes the most important factor in further growth and shape modification. This remodelling is mostly influenced by the masticatory muscles, either directly through periosteal functional matrices in the area of attachment or indirectly as loading of bones causes bending or torsion stresses. Further influence comes from the changing form (shape and size) of the growing elements of the anterior cranial base and the facial skeleton.

The facial skeleton is made up of numerous bones joined by sutures. Growth at the sutural margins is believed to be secondary to bone displacements influenced by capsular functional matrices such as the orbital and nasal capsules. Different parts of individual bones may be influenced by different functional matrices. The maxilla, for example, is influenced by most of the functional matrices acting on the facial skeleton: orbital, nasal, basal, pneumatic and alveolar. In turn, the orbital unit responds to the growing eyeball, the alveolar to the development of the teeth etc. Additionally, the masticatory muscles and other periosteal matrices influence bone surface remodelling.

Growth at facial sutures ceases on average at 17 years of age, which is 2 years earlier than growth of the mandibular condyle and total body height (Björk 1966). In addition developmental skeletal changes in the face slow markedly in girls not long after puberty, but in boys not until late adolescence (Enlow and Hans 1996), this difference is related to the development of facial sexual dimorphism in the teenage period.

Analysis of growth

Thorough understanding of the differences between adult crania therefore depends on study of growth changes in size and shape. Quantitative analyses of cranial growth are, however, not straightforward. Many methodological difficulties are presented in dealing with complex variations in size and shape such as are found between growing and adult crania.

For example, a common approach to the study of growth is through cephalometric radiography and comparisons of superimposed radiographic tracings at different ages. There is, however, no biologically or statistically 'correct' method of superimposition and each researcher has to use as a reference the landmarks or planes that seem most appropriate to the study at hand (Broadbent 1996). The registration method inevitably introduces problems in interpretation in that all landmarks will appear to move away from the registration plane. This makes different studies difficult to compare. One solution (Björk 1968) is to position metallic implants in the developing craniofacial skeleton that can be followed longitudinally on radiographs. Their movements indicate directions and magnitudes of bone displacement and changes in bone orientation. This method has proved valuable in craniofacial research but is limited by the areas in which implants can be safely positioned (especially in the facial skeleton where developing teeth can shift them) and the ethical constraints in repeated radiography.

An alternative is to dispense with data relating to geometric relations of bony points and to focus instead on the distances between such points. Using such measurements it is possible readily to compare growth in lengths but more difficult to thoroughly appreciate the full three dimensionality of growth processes. Recent advances in methodology do, however, show some promise in dealing with the issues of registration and geometry. The application of these methods is the focus of this chapter and we illustrate them through a study of differences in adult cranial morphology and growth allometry between two closely related human populations.

The study populations: Alaskans and Aleutians

The groups being compared in this analysis came from two distinct, but closely related archaeological populations: Aleutians from the Kagomil and Shiprock Islands and Inupiaq Eskimos from northwest Alaska. The two populations are thought to have arisen from a common Proto-Eskimo-Aleut Group that split *ca.* 3000 years ago (Heathcote 1986). Despite their close relatedness the two populations have quite distinct craniofacial morphologies (Fig. 6.1), the Aleut skull being shorter, broader and lower than that of the Inupiaq in addition to possessing less pronounced brow-ridges, a low sloping forehead and no sagittal keel (Hrdlička 1945).

The example geometric morphometric study presented here aims to test two hypothesis.

H1: The first is relatively straightforward; that the adult crania of these populations do not differ in morphology. This is addressed through an examination of the degree of difference between adult means.

H2: The second hypothesis depends on the first being falsified; that the differences between adult populations arise through different growth allometries. This will be tested by modelling shape changes with growth in size (growth allometry) and with increasing dental age in each and comparing these models.

The skeletal material studied consists of 35 crania from the Kagomil and Shiprock Islands in the Aleutians (24 subadults and 11 adults from the National Museum of Natural History, Smithsonian Institution, Washington DC), collected by A. Hrdlička in the late 1930s (Hrdlička 1945); and 43 crania from northwest Alaska (9 adults from the Natural History Museum, London, and 34 subadults from the American Museum of Natural History, New York). The adult northwest Alaskan crania are mostly donations to the Oxford skeletal collection, now housed at the Natural History Museum, London; the subadult Alaskan crania are all from Point Hope and Point Barrow in northwest Alaska. They were collected in 1932 by J.A. Ford (Ford 1959) and in the 1940s by H. Larsen and F. Rainey (Rainey 1971). The cultural affinities of the skeletons were determined by accompanying grave goods as well as general physical appearance of the skeletons.

Crania were selected so as to represent the broadest possible age range between 1 year and adulthood. In total 11 of the Aleutian and 9 of the Alaskan crania were full adult. Sampling at the youngest ages proved difficult because of the paucity of well-preserved very young crania, hence the youngest specimen has a dental age of 1 year. The individuals were aged

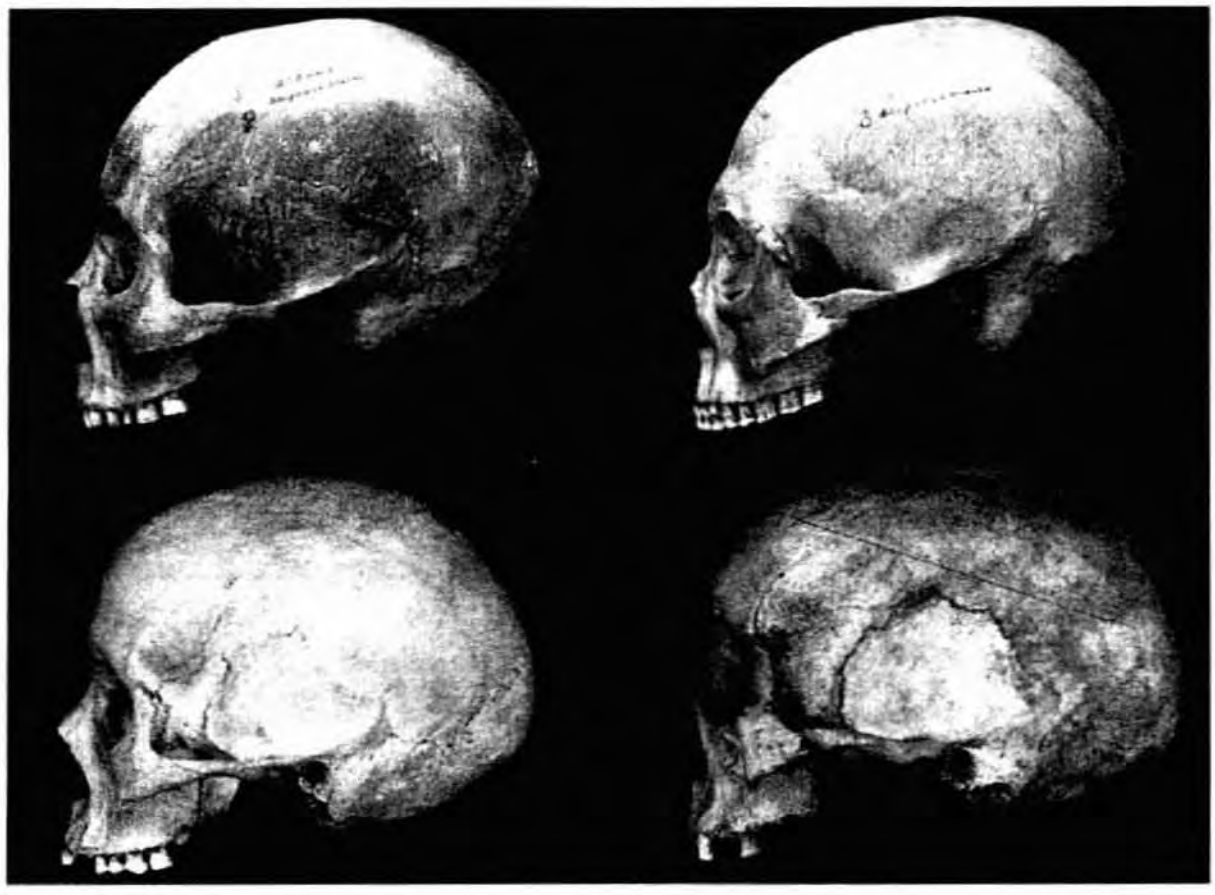


Fig. 6.1. Examples of Alaskan and Aleutian crania. Left, females; right, males; top, Aleutians; bottom, Alaskans. Not to scale.

according to their dental eruption patterns, using the revised standard of Ubelaker (1989) for 'non-white' populations. This standard is compiled from 17 other populations, the standards for deciduous dentition being based on American Caucasians and those for adult dentition on Amerindians. Where possible, because of loss of alveolar bone, crown and root formation stages were used to refine estimates based on eruptions. It is recognised that such data lead to relatively crude age estimates, but this is a practical limitation that would have required considerable resources in terms of radiology and dental histology to overcome and with dubious end benefits in terms of the conclusions of this study.

Quantification of morphology

The issue of measurement is frequently considered to be a rather straightforward matter: simply take calipers to specimens and record relevant lengths. In this chapter, we take the opportunity to consider measurement more deeply. First, it is necessary to define some basic terms: form, shape and size.

Unless they are identical, sets of measurements describing objects or figures will differ in their absolute scale, in their proportions and, if the measurements are taken with reference to the surroundings, in location and rotation (reflection also comes into play in some situations). We use the term 'form' to refer to the spatial organisation of an object independent of its location ('translation' is the term used for differences due to location) and rotation. Form itself we subdivide into two components 'size', which is a measure of scale of the form and 'shape' refers to aspects of form independent of scale. The term 'registration' is used to refer to the way in which objects are translated, rotated and scaled with respect to each other.

These definitions lead us to seek a biologically sensible quantitative representation of the spatial organisation of each cranium. Landmarks form the basis of most morphometric analyses. There are, however, numerous practical issues surrounding their identification and philosophical issues surrounding their nature. Principal amongst the latter is the issue of equivalence from specimen to specimen.

In biology a special type of equivalence forms the basis of many studies, homology (Hall (1994) provides a recent review). Homology in evolutionary studies relates to the matching of parts between organisms according to common evolutionary origin. In developmental studies, however, 'homology' is used in a different sense to refer to the matching of structures through ontogenetic time. This matching is not necessarily physical, since local growth phenomena (e.g. bony remodelling, shifting muscle insertions) may result in replacement of material between different ages such that structures that appear equivalent in terms of their local relations need not necessarily reflect the location of homologous material. Wagner (1994) has recently noted that, despite material replacement, structural identity is maintained. This maintenance of identity requires the action of 'morphostatic' mechanisms and, although structures may not be equivalent in the sense of material, they may be equivalent in terms of the continuity of morphostatic mechanisms. Developmental equivalence between landmarks may therefore be considered to equate to homology in the sense of van Valen (1982): 'correspondence caused by continuity of information' – a homology of the processes giving rise to structure.

In morphometric studies of growth we are faced with the task of representing the spatial relations of developmentally homologous parts in a suitable way. The classic approach is through the use of landmarks defining the limits or meeting points of structures (e.g. Martin 1928; Trevor 1950). Landmarks are samplings of the map of homologies between specimens (Bookstein 1991) and the density with which landmarks can be sited in regions of a specimen is dependent on the resolution with which the

homology map can be discerned. This definition of the homology map depends, in turn, on purely biological rather than mathematical or geometric criteria. The identification of landmarks on the homology map may, however, depend on geometric features. The practical difficulties in identifying landmarks are recognised in a commonly quoted taxonomy of landmarks that is designed to encourage critical appraisal (Bookstein 1991; Marcus *et al.* 1996). Below we summarise and modify it slightly.

Type I landmarks are those whose homology from case to case is supported by the strongest (local) evidence (meeting of structures or tissues; local unusual histology etc.).

Type II landmarks are those in which claimed homology from case to case is supported by geometric, not histological evidence (tooth tip etc.). Type II landmarks include landmarks that are not homologous in a developmental or evolutionary sense but are equivalent functionally, such as wing tips.

Type III landmarks have at least one deficient coordinate (which means that they can be reliably located to an outline or surface but not to a very specific location, e.g. tip of a rounded bump).

In terms of the homology map therefore we can be most confident about landmarks of type I and least about landmarks of type III. This should not necessarily preclude the use of all types of landmark but it should lead us to expect greater (possibly directional) variation due to error alone in data based on type III rather than on type I landmarks when interpreting the results of analyses.

Landmarks in the study populations

In our example study of Aleutians and Alaskans we quantify the morphology of each face using 26 landmarks per half face. Most of these are of type I, some of type II and a few of type III. Their name and type is listed below (definitions in Martin 1928; Trevor 1950; where no definition exists we give brief details): alare, III; alveolare/infradentale superius, II; bregma, I; dacryon, II; frontomalare orbitale, II; frontomalare temporale, II; frontotemporale, III; glabella, III; infraorbital foramen upper boarder, III; jugale, II; maxillofrontale, I; nasion I; nasospinale, II; orbitale, III; point at which the palatine-maxillary suture crosses the midline (pmx), I; staphylion, II; stephanion, II; most superior point on rim of the orbit, III; midpoint supraorbital torus, III; the external alveolus at the distal margin of the canine (deciduous or permanent), II; the external alveolus at the distal

margin of the most posterior tooth in the tooth row, II; the external alveolus at the distal margin of the second incisor (deciduous or permanent), II; zygomaxillare, II; zygoorbitale, II; zygotemporale inferior, II; zygotemporale superior, II.

Landmark coordinates were taken in no particular registration using a Polhemus 3 Space Isotrak II digitiser (Polhemus Incorporated, 1 Hercules Drive, PO Box 560, Colchester, VT 05446, USA). This operates electromagnetically through detection of the location and orientation of a coal within a pointing stylus relative to three reference coils. Tests of accuracy using a cube of known dimensions indicate that measurements of coordinates are accurate to within approximately 0.5 mm, although this figure varies according to ambient electromagnetic conditions. All data were gathered by one of us (U.S.V.).

Analysis and modelling of form transformations in growth and evolution

Once landmark data are gathered, the task of analysis can begin. In this study, adult differences and growth allometry are to be addressed. In particular we wish to investigate changes in cranial shape with increasing size and age during growth. It is therefore necessary to partition size from shape, and the calculation of a size measure and appropriate scaling of forms are called for. Following scaling, analyses can be directed to the study of covariances between shape, age and size. Interpretation can then proceed through examination of significance statistics and, importantly, through visualisation of the analytical results.

Size

Interlandmark distances, like the coordinates of landmarks are dependent on both size and shape; form = size + shape. When the focus of interest is growth it seems sensible to partition form into size and shape and to examine the relationship between these, but this presents several difficulties.

Size is not a straightforward quantity and there are difficulties in discussing size independently of shape in most circumstances. One difficulty arises because 'size' is often loosely defined. Sneath and Sokal (1973) ask 'which is bigger, a snake or a turtle?'. The term 'size' in this instance might relate to the differences in scale over whole objects. A suitable size measure is one

that relates to the magnitude of many dimensions such as their sum or their mean.

In analyses of form (size + shape) based on landmark coordinates such as we undertake in this chapter a mathematically natural size measure is centroid size, the summed deviation of landmarks from the mean of all landmarks (centroid). Size measures may be chosen because they are appropriate, given the hypothesis at hand. There are no absolutely 'correct' choices in every circumstance, yet different choices may lead to different conclusions. If shape variations amongst specimens are fairly small with respect to size differences, the differences in result through different choices of size measure will also be small. As such, the same biological conclusions will be reached through different approaches.

The relationship between size and age in our study populations

In our example study we choose centroid size as an appropriate measure of scale. Centroid size is sensible biologically, since it takes account of the overall spread of landmarks and so of scale in a general sense. Of interest is the relationship between scale and estimated (dental) age in each of the Alaskan and Aleutian samples.

Figure 6.2 is a plot of deviation from the mean centroid size (cm; vertical axis) against estimated age (years; horizontal axis) for the two populations. No attempt was made to estimate the ages of specimens beyond the possession of fully erupted and occluded permanent dentition and fused spheno-occipital synchondrosis; as such, adults are simply allocated a nominal age of 21 years or more. In consequence they show a range of variation in centroid size but are represented in a vertical scatter above the 21 year mark on the horizontal axis. The scatters are such that Aleutian adults appear to show a wider spread and marginally larger mean centroid size. A t-test indicates, however, that the apparent difference between means is not significant ($p = 0.1$) although the variance ratio indicates that Aleutian adults are significantly more variable in centroid size than are the Alaskans ($p = 0.015$).

Amongst the subadult specimens there is a highly significant correlation between centroid size and age ($r = 0.92$, $p < 0.001$). There is no apparent difference in this scaling relationship between Alaskans and Aleutians below the estimated age of 10. The rate of increase in size with age appears to diminish after the age of 10 years in the Alaskan sample. We lack sufficient data from Aleutians in their teens to determine whether this is the same in both populations. The increased size variability amongst adult

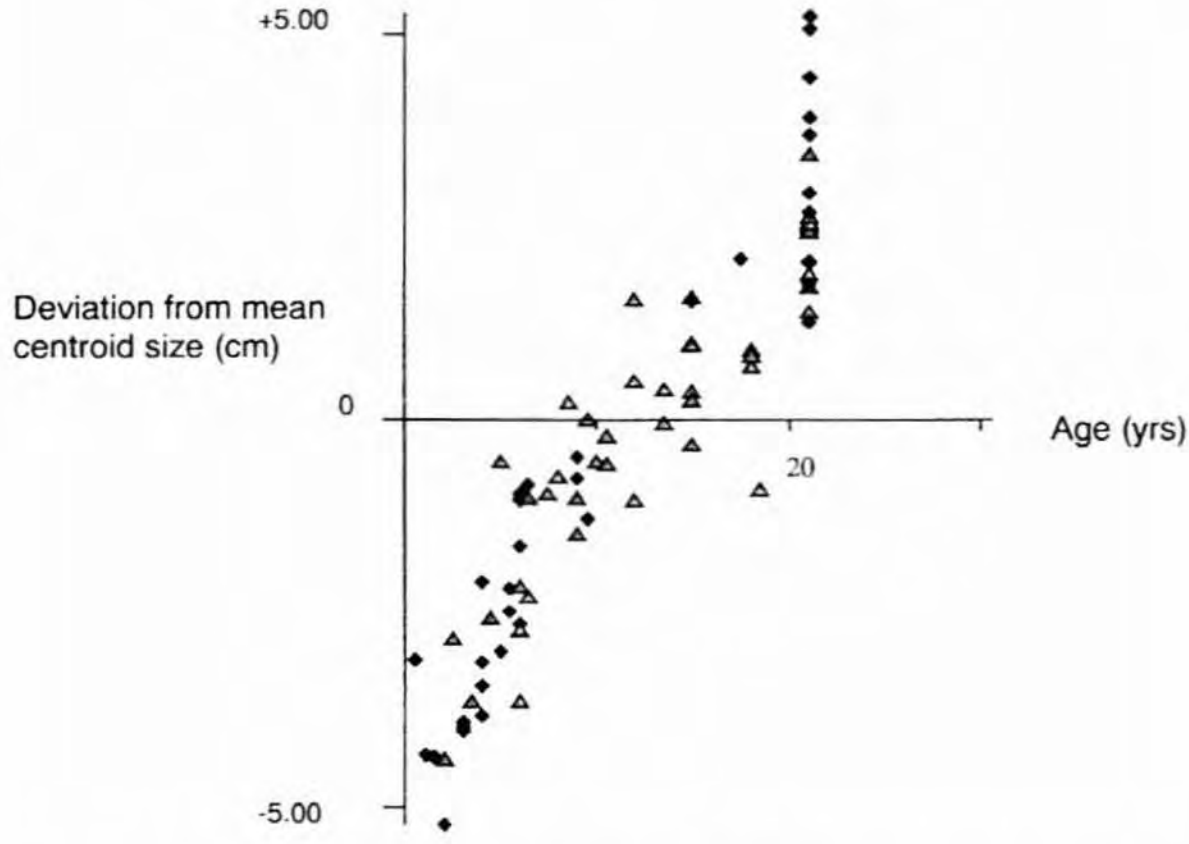


Fig. 6.2. Plot of dental age (horizontal axis) vs. deviation from mean centroid size (vertical axis). Triangles, Alaskans; diamonds, Aleutians; r between age and size = 0.92, $p = 0.001$.

Aleutians may be due to differences in later growth but this also remains an open question because of lack of data.

These findings lead us to consider whether any differences in shape exist between adult Aleutians and Alaskans. If there is any evidence of differences, are these due to differences in growth allometry or are they present at birth and simply continued into adulthood?

Shape

In this chapter we focus on the analysis of form variations using landmark co-ordinates and use statistical tools from geometric morphometrics (Bookstein 1991; Marcus *et al.* 1996). Classically, however, landmarks form the basis of analysis of variations in form through the taking of interlandmark distances ('ilds'). This is because ilds are independent of location and rotation of the forms under comparison and they are very easy to acquire using calipers. Furthermore ilds in themselves often conform to the biological notion of a 'character' or feature of interest.

Multivariate morphometric methods (Sneath and Sokal 1973; Mardia *et*

al. 1979) allow relationships amongst specimens to be examined on the basis of several ilds simultaneously. If sufficient ilds ($k(k-1)/2$, for k landmarks) are taken or fewer ilds are taken in a systematic way (e.g. in the form of a truss; Bookstein *et al.* 1985), then it is possible to generate the original landmark coordinates from the matrix of ilds through multidimensional scaling (Mardia *et al.* 1979). In turn, this allows the visualisation of the results of an analysis in terms of co-ordinate representations. Rao and Suryawanshi (1996) have recently considered appropriate approaches to the multivariate analysis of form variations using such sets of ilds. These include principal components and canonical analysis.

An alternative set of approaches to the analysis of form variations through the use of ilds has been developed by Lele (1993). These approaches are collectively known as Euclidean distance matrix analysis (EDMA). EDMA allows form variation to be examined through the comparisons of ratios of pairs of equivalent ilds between specimens. It results in large matrices of ild ratios that can be turned both to the identification of landmarks which appear to differ significantly in relative location between forms and to analyses of growth (Richtsmeier *et al.* 1993). This identification depends on the careful examination of often very large matrices of form differences, growth differences etc. and visualisations of such differences can be achieved using multidimensional scaling to generate landmark coordinates of interesting forms.

In examining ilds rather than co-ordinates, issues concerning registration are to some degree sidestepped; however, visualisation and interpretation of results are somewhat more difficult and issues arise relating to the estimation of means, scaling and the morphometric space in which statistical inference is to be undertaken. Lele (1993) argued strongly in favour of EDMA and against registration based approaches such as those used in this study. Many other statisticians and biometricians place confidence in registration-based approaches (see e.g. Bookstein 1978, 1987; Marcus *et al.* 1996; Dryden and Mardia 1998).

In this chapter we focus on methods for the direct analysis of landmark co-ordinates because these directly address geometry, are the best understood at present and form the focus of much current interest (e.g. Marcus *et al.* 1996; Dryden and Mardia 1998).

Geometric morphometrics

Approaches to analysis based on landmarks are fundamentally different from those using ilds in that differences in co-ordinate values due to

location and orientation alone (registration) need to be factored out of the comparison. We aim to preserve geometric information throughout the analysis and the class of approaches known as geometric morphometrics or statistical shape analysis is appropriate for this purpose (Rohlf and Bookstein 1990; Marcus *et al.* 1996; Dryden and Mardia 1998).

The task of describing relative landmark movements has proved intractable until recently. In the space of the original specimens (the real world) all landmarks will appear to 'move away' from the reference points chosen for the superimposition and so different registrations will appear to indicate different patterns of growth. In terms of multivariate statistical analysis of registered co-ordinate data, the particular patterns of variation represented by a particular principal component or canonical axis will be entirely dependent on the way in which operational taxonomic units (OTUs) have been registered with respect to each other.

Thus, the perceived displacement of any particular landmark from one shape or another depends upon the way in which OTUs are scaled, reflected, rotated and translated with respect to each other. Different registrations will produce different impressions of the shape transformations and regions close to the registration points will appear to change less than those more distant. These difficulties are most significant when the shapes under comparison are very different and unimportant when they are very similar. The important issue is therefore not one of choice of registration method but rather of the magnitude of differences in shape. When variations are small, the effects of registration method are also small. Dryden and Mardia (1998, p. 287) give a tentative suggestion that 'if the data lie within full Procrustes distance of about 0.2 of an average shape then methods give very similar conclusions'.

Procrustes registration

Given small variations in shape we seek a registration method that is sensible in terms of biology and well understood statistically. Unless we have an *a priori* basis for selecting a particular fixed baseline, and in our example facial data we do not, it is reasonable to register forms on the basis of a 'best fit' of all landmarks. The methods of Procustes analysis (reviewed by Rohlf and Slice 1990; Dryden and Mardia 1998) register forms by translating, rotating, reflecting and scaling forms with respect to each other to maximise fit.

In Fig. 6.3a we illustrate the results of Procrustes registration of the co-ordinate data from adult Aleutian and Alaskan crania included in the

example study. It is difficult to appreciate the full three-dimensional geometry of the resulting landmark clusters but it is clear from Fig. 6.3a that the scatters of registered landmarks are fairly small. Figure 6.3b illustrates a wireframe model drawn between mean coordinates. It gives a clearer impression of the three-dimensional nature of our data and it is drawn such that approximate boundaries of the palate, maxilla, frontal and zygomatic bones are indicated.

Registered sets of coordinates can be interpreted visually but it is usually desirable to undertake statistical analyses and model shape variability in an abstract 'shape space'. The shape space for Procrustes registered data is non-linear and statistical analysis needs to account for this.

Statistical analysis of Procrustes registered data

When figures (described by k landmarks in m dimensions) are scaled (centroid size = 1) and registered to remove translational and rotational differences by generalised least squares superimposition (generalised Procrustes analysis; Gower 1975; Rohlf and Slice 1990; Goodall 1991) they can be represented as points in a shape space which is of $km - m - m(m-1)/2 - 1$ dimensions ($= km - 7$ when $m = 3$; $= km - 4$ when $m = 2$). This dimensionality arises because location (m dimensions), rotation ($m(m-1)/2$ dimensions) and scale (1 dimension) differences have been removed.

This space was first described by Kendall (1984) and it is commonly referred to as Kendall's shape space. We have already noted that the relative locations of points representing specimens in this space are more or less independent of registration if variations are small. Additionally and importantly from a statistical perspective, isotropic distributions of landmarks about the mean results in an isotropic distribution of points representing specimens in the shape space. Kendall's shape space is, however, non-Euclidean (non-linear). For the most simple shapes, populations of triangles, the space can be visualised as being spherical but for more than three landmarks the space is much more complex, being high dimensional (Le and Kendall 1993).

Since the shape space is non-linear, great care is needed in carrying out statistical analyses. One approach that is particularly appealing, since it naturally allows the study of multivariate allometry, is to carry out principal components analysis (PCA) in the tangent space to Kendall's shape space (Dryden and Mardia 1993; Kent 1994). For triangles we take the scatter of points on the spherical shape space representing variation within our sample and project it into a Euclidean tangent plane in exactly the same way as a cartographer might project a map from a globe onto a flat

sheet of paper. The co-ordinates of the points representing specimens are no longer given in terms of the sphere but rather as co-ordinates in the plane. As long as the projection has not resulted in excess distortion (as might occur if the projection encompasses a large proportion of the sphere) we can carry out useful analyses in this plane. For higher dimensions the tangent plane to the shape sphere can be imagined as a tangent space of $km - m - m(m-1)/2 - 1$ dimensions.

Procrustes tangent co-ordinates can be estimated using the Procrustes tangent space projection given by Dryden and Mardia (1993). This projection results in a $(k-1)m$ vector of tangent space shape co-ordinates with respect to the mean for each specimen. Both of these vectors of tangent space co-ordinates are of rank $km - m - m(m-1)/2 - 1$. Principal components analysis can be carried out using tangent space co-ordinates to extract $km - m - m(m-1)/2 - 1$ eigenvectors; the principal components of variation of shape. In the case of a growth study we expect that the first few principal components will serve as an adequate model of allometry. Note that since Procrustes analysis involves scaling to centroid size the variations we examine through PCA are shape rather than form variations. If we wish to examine the relationship between size and shape (allometry) we can do this by examining plots and correlations of principal components (PC) scores vs. centroid size for the significant principal components.

Visualisation of patterns of shape variation

Variation in the shape space

Since the PCs are mutually orthogonal they each represent statistically independent modes of variation in the sample. Further interpretation of the PCs depends in part on visualisation of the shape variation represented by each. A graphical representation of shape variation along each axis can be achieved by reconstructing hypothetical specimens with scores of 0 on all PCs except the PC of interest. By inspecting a range of scores on this PC it is possible to visualise the variability along it through series of reconstructed forms or as an animation.

Transformation grids

An alternative strategy for comparing co-ordinate representations of form is to represent differences in a single diagram as a deformation that smoothly rearranges the configuration of landmarks as a whole. The best known representation of such a deformation is in the form of a 'Cartesian

transformation grid' (Thompson 1917) in which differences in morphology are described through distortions of a regular grid.

An appropriate approach to drawing transformation grids uses mathematical functions, known as thin plate splines (TPS: Bookstein 1989; Marcus *et al.* 1996; Dryden and Mardia 1998). The grids derived from TPS indicate how the space (or a regular Cartesian grid) in the vicinity of a reference figure might be deformed into that surrounding a target such that landmarks in the reference map exactly into those of the target. The thin plate spline ensures that this deformation involves minimum bending; and it is chosen for this purpose, since this seems a sensible minimisation criterion. The statistical and graphic models of shape transformations which result from these approaches are readily interpretable and highly visual (e.g. Bookstein 1978, 1989; O'Higgins and Dryden 1992, 1993; Marcus *et al.* 1996). The thin plate spline is not the only possible choice of method for drawing a grid but the fact that it minimises 'bending energy' is intuitively appealing. Besides producing a transformation grid thin plate splines can be extended to examine the affine and non-affine components of shape difference and to explore variation at different scales (localised variations vs. global) amongst OTUs. These refinements are beyond the scope of this chapter but full accounts have been given by Marcus and colleagues (1996) and Dryden and Mardia (1998).

Geometric morphometric analysis of Aleutian and Alaskan craniofacial variation

We illustrate the approaches described above by comparing adult morphology and postnatal growth in the facial skeletons of Aleutians and Alaskans. The first hypothesis (H1) we test is that adults of the two populations do not differ in facial morphology.

Differences between adult Aleutian and Alaskan samples

Figure 6.3a presents the results of Procrustes analysis of adult Aleutians and Alaskans. In this diagram, each point represents the location of a landmark on a specimen. The scatters of points indicate variability at each landmark and this appears to be small. The mean of the landmark configurations is presented in Fig. 6.3b, landmarks are joined by lines indicating approximate boundaries of the frontal, zygomatic, maxilla and palate.

Principal components analysis of the tangent coordinates results in the

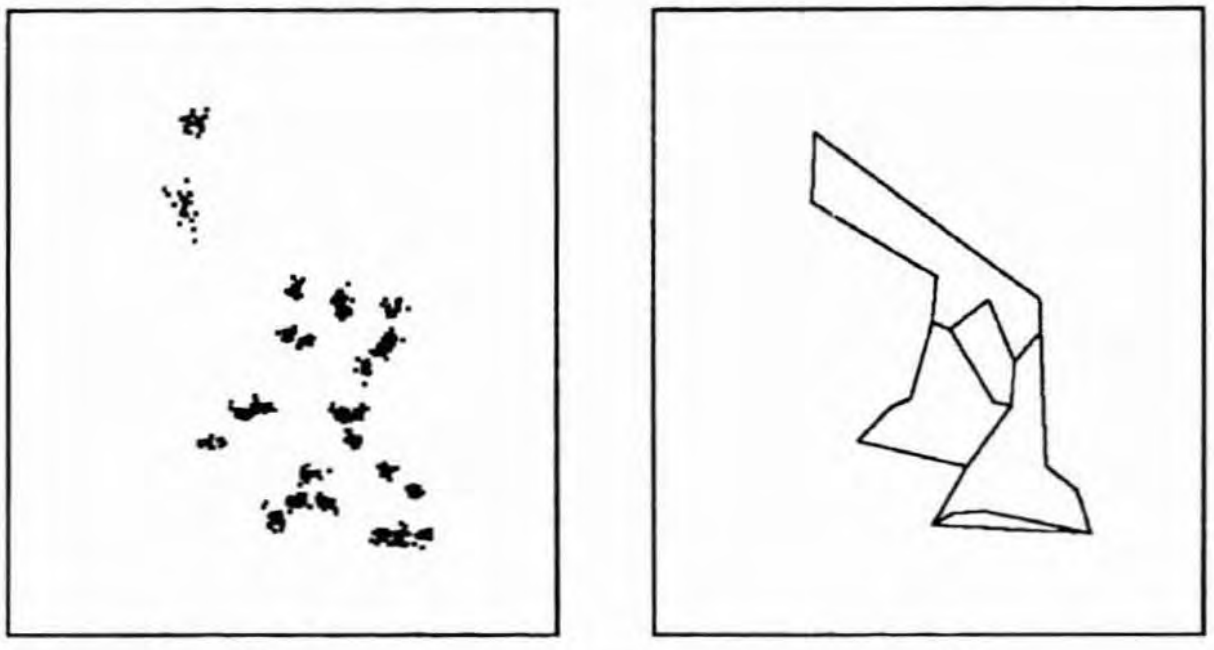


Fig. 6.3. Left frame (a), scatter of points representing adult facial shapes after generalised Procrustes registration. Right frame (b), the mean of all adult faces with landmarks connected by a wire frame approximately outlining facial bones.

scatter of specimens on PCs I and II presented in Fig. 6.4. In this plot, the Alaskans are completely separated from Aleutians such that Alaskans occupy the upper right-hand side of the plot and Aleutians, the lower left. This leads us to consider that the differences between adults might be significant, although small sample size in relation to the rank of the shape space does not allow conventional statistical testing of these differences (such as might be carried out using Hotelling's T^2). An alternative approach is through a permutation test (Good 1993) in which the true difference between adult means is compared with the range of differences between the means of many randomly permuted samples drawn from the same data. In total we have only 20 specimens, so the number of permutations we can draw is rather small; however, different runs of the permutation test over 100 permutations indicate that the adult means are significantly different at a level of $p < 0.01$. H1 is falsified.

Having established that the adult means are different we turn to an examination of the nature of these differences. In Fig. 6.5 configurations of landmarks in lateral view are represented as rendered images constructed through triangulations of landmarks. Figure 6.5a represents the Alaskan mean and Fig. 6.5c the Aleutian mean. In Fig. 6.5b the difference between these means in represented by the transformation grid calculated using a three-dimensional thin plate spline. This is drawn in a single plane just to the right of the midline since it is in this plane and in this region that the

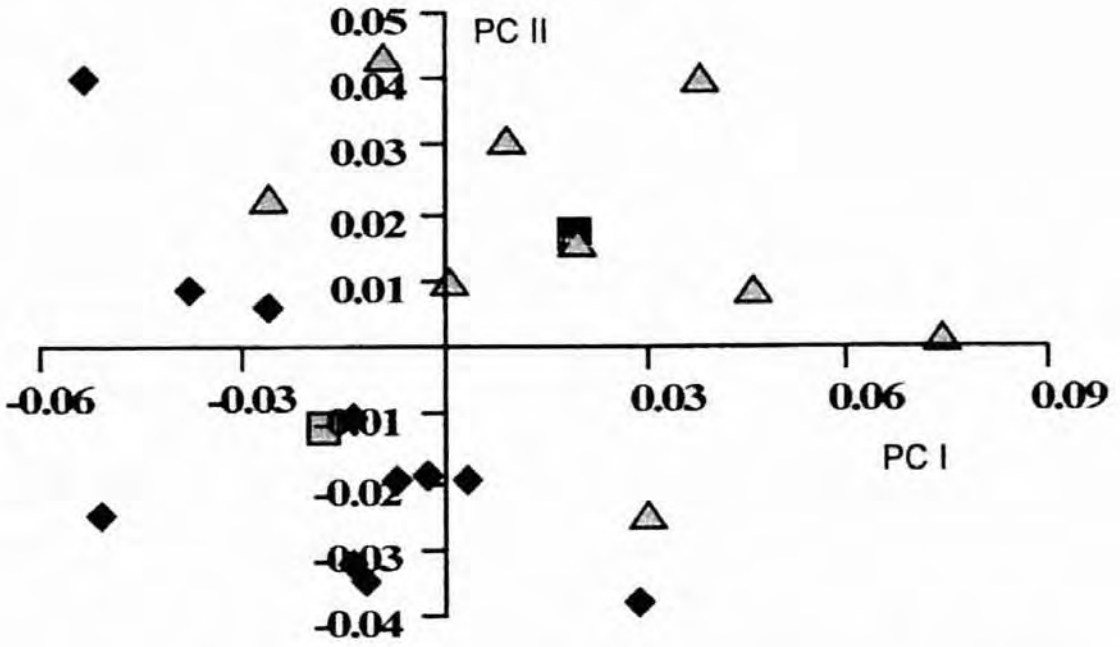


Fig. 6.4. Principal components analysis of adult data after generalised Procrustes registration. Triangles, adult Alaskans; black rectangle, mean adult Alaskan; diamonds, adult Aleutians; grey rectangle, mean adult Aleutian. Horizontal scale, PC I 24% total variance; vertical scale, PC II 16% total variance.

differences appear greatest in magnitude. The grid was regular rectangular over the Alaskan mean (the reference shape) and its deformation to the Aleutian mean (target shape) is multiplied by a factor of 2 for ease of interpretation. It can be seen that in this plane, the principal difference between Aleutian and Alaskan means consists of a relative midfacial and nasal projection in Aleutians with respect to Alaskans. The transformation grid showed little distortion in the coronal and transverse planes other than that already noted in the vertical. We conclude therefore that Alaskan and Aleutian adult faces differ significantly and that these differences consist principally of a more prominent prognathism of the midface and projection of the nasal region in Aleutians with respect to Alaskans.

The ontogenetic basis of differences between Alaskans and Aleutians

Despite a relatively short period of isolation of 3000 years or so the adults of these two populations present different facial morphologies. It is of interest to investigate the ontogenetic basis of these differences since the results will reflect on evolutionary and adaptive mechanisms in the face. Several possible explanations exist for the differences we encounter between adults;

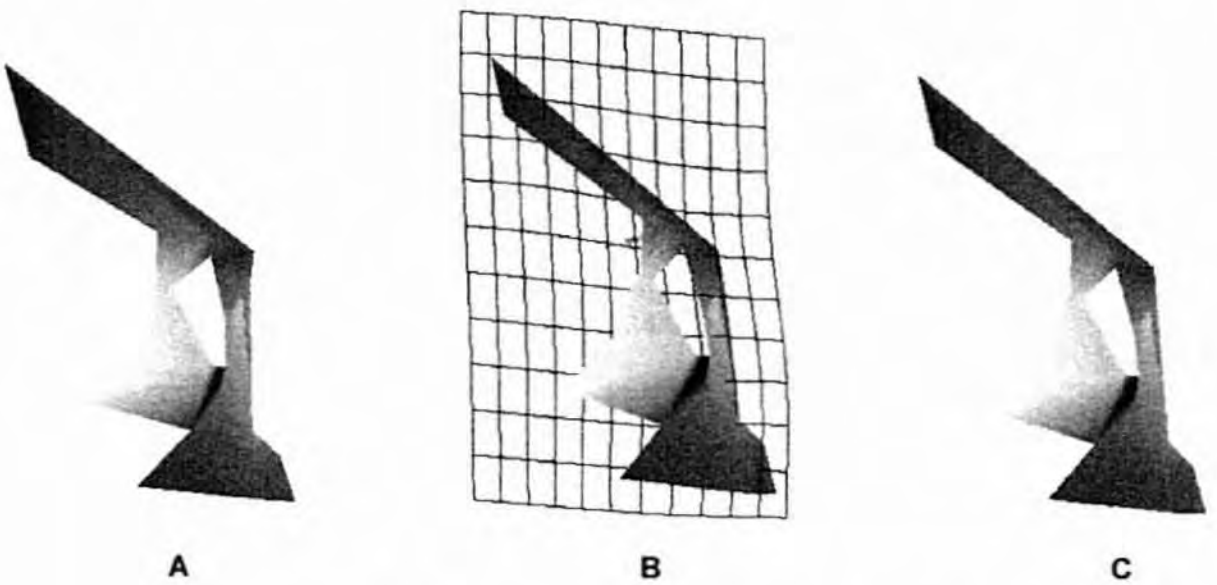


Fig. 6.5. The contrast between Alaskan and Aleutian adult means. (a) Alaskan mean; (c) Aleutian mean; (b) Cartesian transformation grid illustrating the difference between Alaskan (reference) and Aleutian (target) means. The deformation between Alaskan and Aleutian is emphasised for the purposes of drawing the grid by multiplying the transformation by a factor of 2. Permutation tests give a significance of $p < 0.01$ for this difference in means.

Differences may be present at birth and these may persist into adulthood, postnatal growth allometries being identical between the populations.
Populations may be identical at birth and diverge through different growth allometries.
Populations may be identical at birth and diverge through relative extension/truncation of a common growth trajectory.
Some combination of the above might operate in concert.

This study sets out to test the hypothesis (H2) that different growth allometries exist between the populations. If this is falsified we can examine the nature of differences between populations at birth and the extent to which growth is relatively extended or truncated between the populations.

We begin the study of growth changes in facial shape by undertaking a Procrustes analysis of the whole data set: infants, juveniles and adults of both populations. The resulting deviations of co-ordinates from the Procrustes mean are then submitted to PCA. The first PC from this analysis accounts for 47.5% of the total variance, the second for 6.2% and the third 5.8%. The first 20 PCs together account for >90% of the total shape variance and there are ($km - 7 =$) 71 non-zero eigenvectors in total. This means that the first, second and third PCs in combination account for 60% of the total shape variance and so can be used to examine the major features of shape variability in the 71-dimensional shape space. Examin-

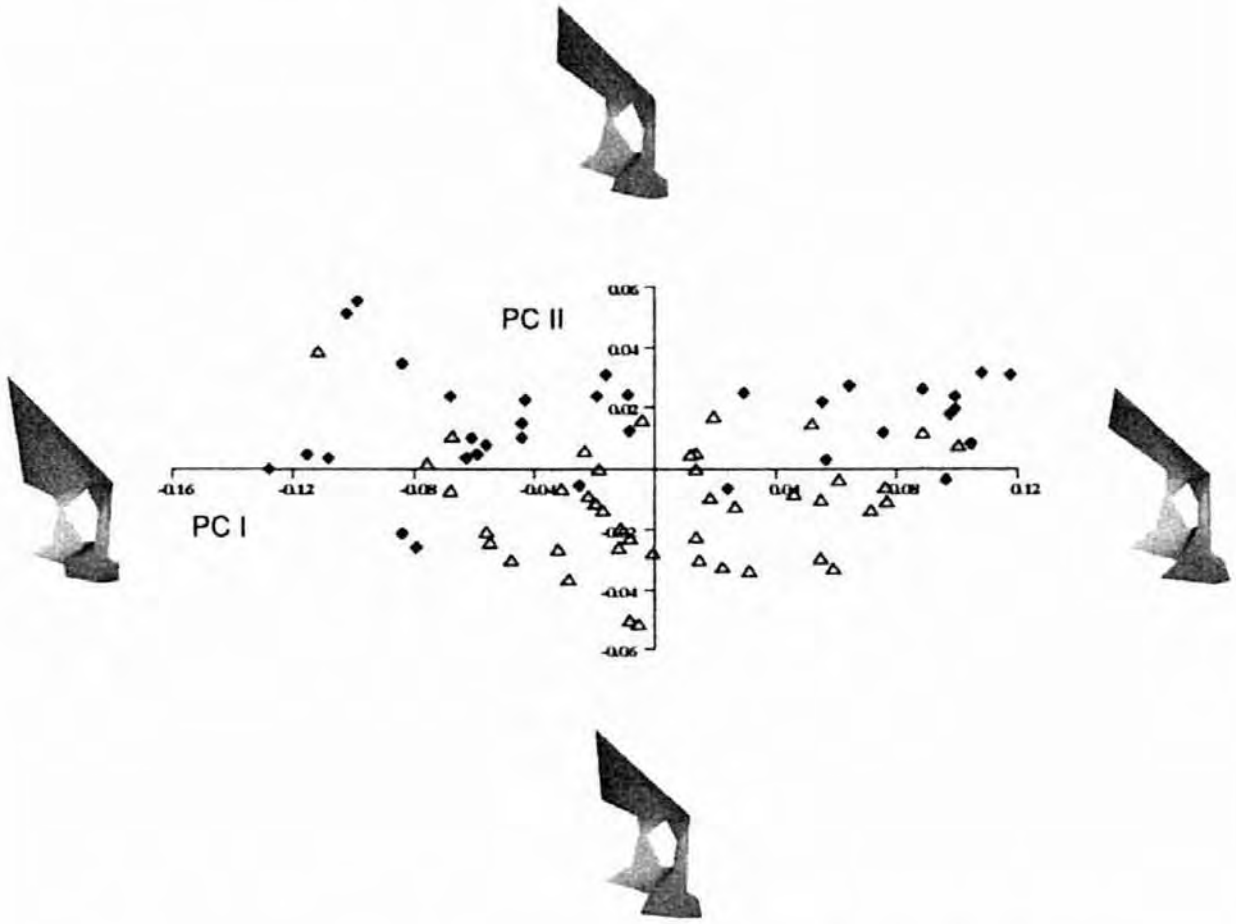


Fig. 6.6. Principal components analysis of adult and subadult data after generalised Procrustes registration. PC I (horizontal axis) vs. PC II (vertical axis). Triangles, Alaskans; diamonds, Aleutians. Small inset figures illustrate shapes represented by scores of $\pm$ 0.12 on PC I and $\pm$ 0.05 on PC II.

ation of PCs of order >3 showed no biologically interesting variation and so we focus on the first three only.

Figure 6.6 presents a plot of the first two PCs. At the extremes of each PC is drawn a rendered reconstruction of the mean configuration after transformation along it. The first PC does not separate Alaskans from Aleutians, rather the reconstructions at its extremes and the ordering of specimens suggests that it represents size-related shape variation during growth (ontogenetic allometry). The reconstructions indicate that it represents a mode of variation in which specimens with low scores are orthognathic, with relatively large orbits, and those at the other extreme are prognathic, with relatively small orbits.

In order to investigate more deeply the biological correlates of variation along the first PC we examine the relationship between scores on this PC and centroid size. Figure 6.7 shows a plot of PC I against centroid size (units are cm) and it seems from this that the two are strongly related. The correlation between scores on PC I and size is 0.91 and this is significant at the $p < 0.001$ level. PC I can therefore be said to represent a mode of facial

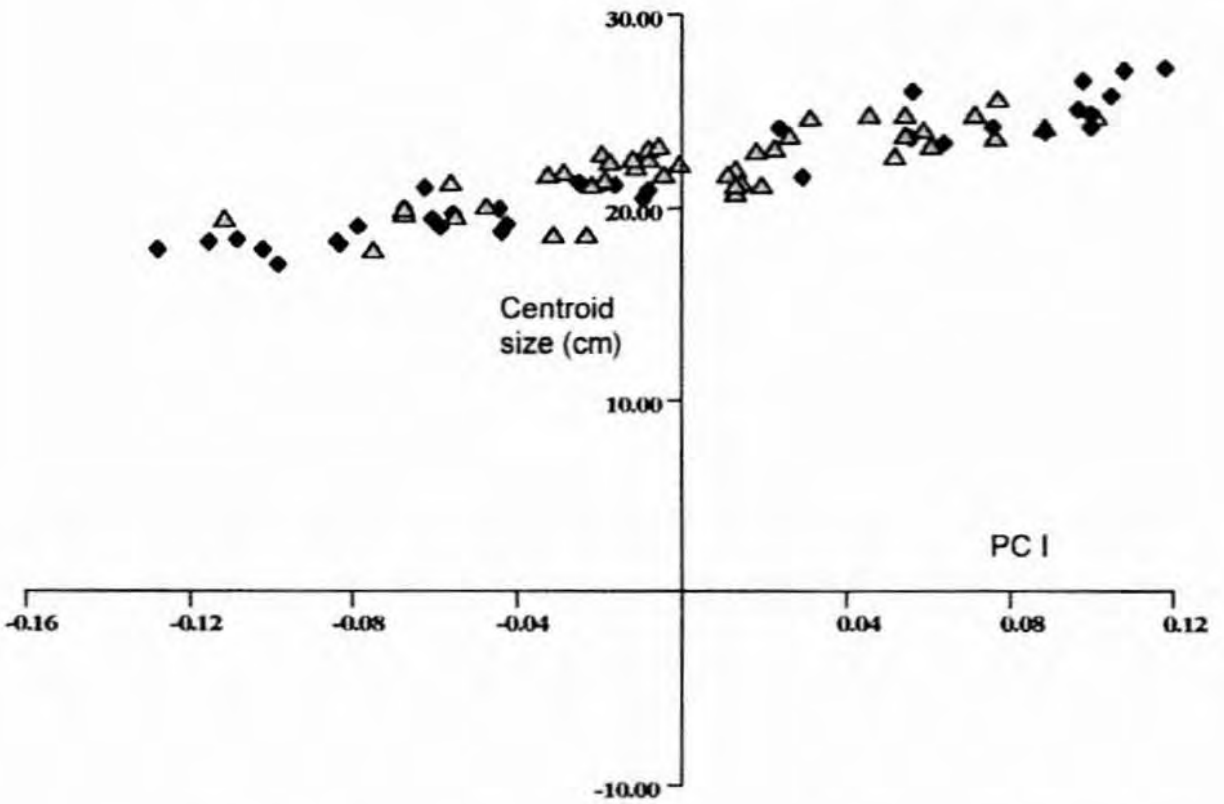


Fig. 6.7. PC I (horizontal axis) vs. centroid size (vertical axis) from the analysis of adult and subadult crania. (See Fig. 6.6 for key.) $r = 0.91$, $p < 0.001$.

shape variation that is strongly related to cranial size variation during growth. As such it is a good model of ontogenetic allometry. It is noteworthy that this relationship appears identical in both populations: there is no evidence of differences in the mean or gradient. No other PC shows evidence of a size-related shape change so we conclude that the allometric relationship observed on PC I is identical for both populations.

One subtle difference is, however, possible in that some adult Aleutians have higher scores on PC I than Alaskans, suggesting that Aleutians may extend the common allometry into larger size ranges. The difference in mean adult scores on PC I is, however, not quite significant ($p = 0.055$).

Of related interest is the relationship between relative dental age and scores on PC I. These are plotted in Fig. 6.8, the vertical axis represents mean dental age in years and the horizontal represents scores on PC I. This plot indicates a relationship between age and the mode of shape variation represented by the first PC. The correlation between these variables, $r = 0.90$, is highly significant, $p < 0.001$. This is not surprising, given that we have already noted a highly significant relationship between age and size. It is noteworthy, however, that age is less strongly correlated with shape than is size. This might be expected, since size and shape are biologically interwoven through growth phenomena while age is simply the temporal axis within which the biological processes occur.

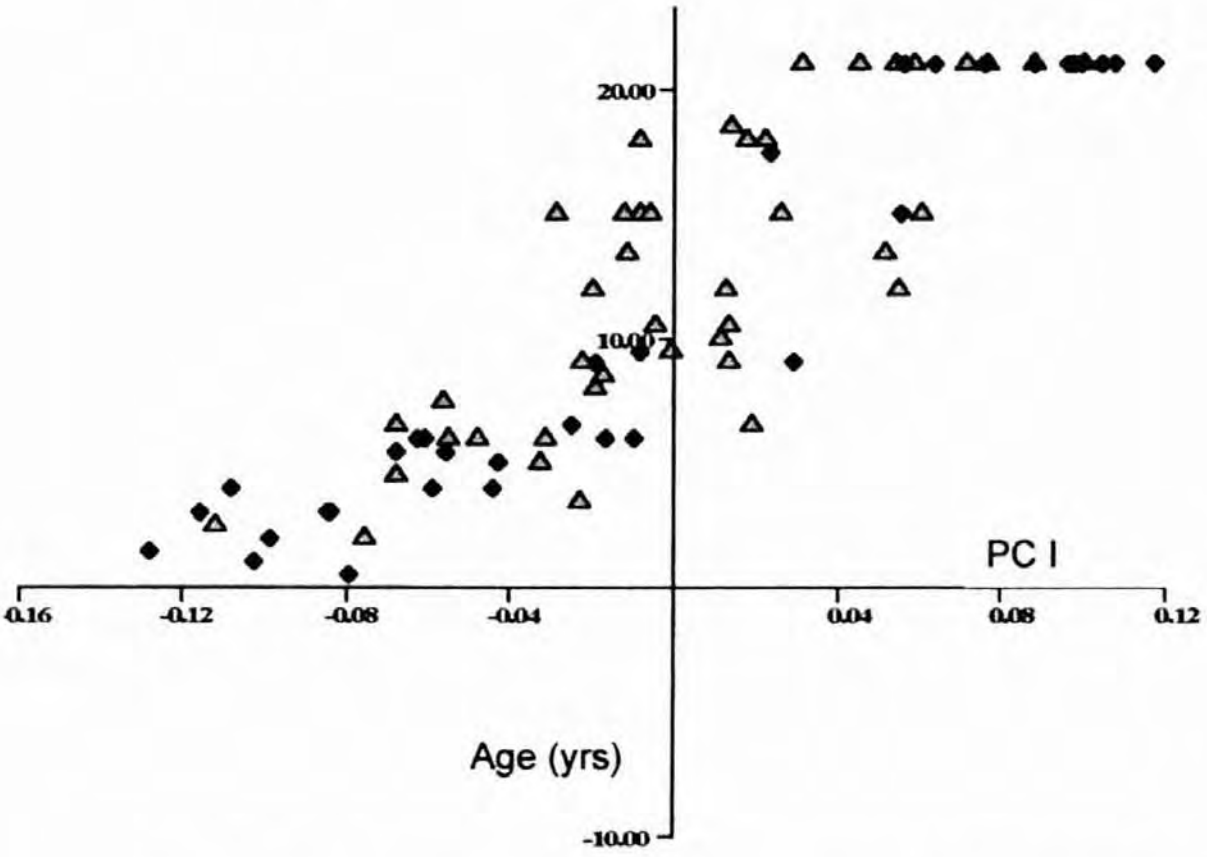


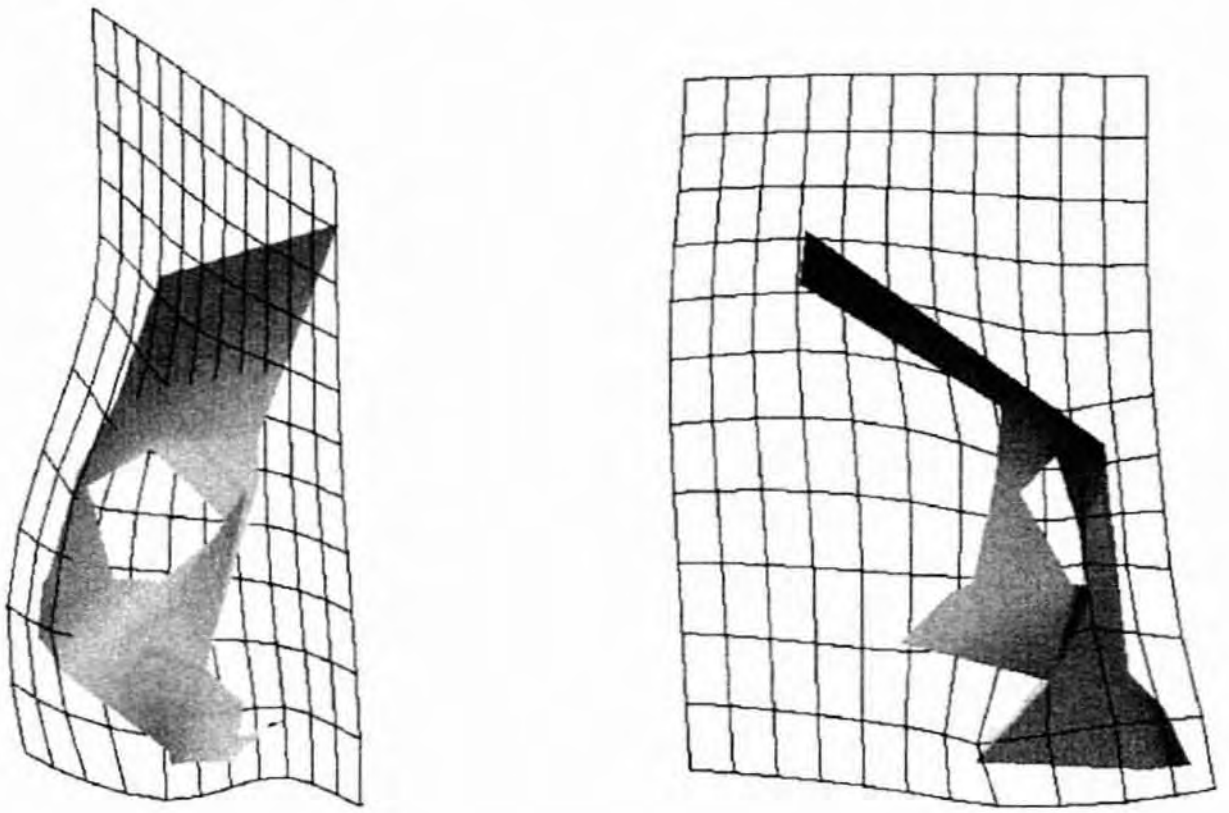
Fig. 6.8. PC I (horizontal axis) vs. relative dental age in years (vertical axis) from the analysis of adult and subadult crania (adults all nominally allocated age 21). (See Fig. 6.6 for key.) $r = 0.90$, $p < 0.001$.

We conclude that the data fail to falsify the hypothesis (H2) that different growth allometries exist between the populations. There is, however, a suggestion that Aleutians extend this common allometry (hypermorphosis) beyond Alaskans but this just fails to achieve statistical significance.

Having demonstrated a common ontogenetic allometry for our study populations it is of interest to examine its nature. We examine the geometric aspects of allometric growth by drawing (Fig. 6.9) transformation grids between small/young (PC I score −0.12; reference shape) and large/old (PC I score +0.12; target shape) specimens.

In Fig. 6.9a a Cartesian transformation grid is drawn in a coronal plane such that it passes through the lateral maxilla and just within the orbit of a smooth-rendered representation of the transformed mean at PC I score 0.12 (mean of oldest and largest specimens). The grid is expanded (principally laterally but also vertically) and curved upwards over the zygomatic part of the maxilla. This indicates that during growth this region undergoes substantial relative increase in size and relative lateral displacement.

In Fig. 6.9b the target form is shown in lateral view and a grid is drawn passing through the middle of the orbit. Its deformation confirms that relative vertical expansion of the maxilla is a feature of growth. The grid is



A B

Fig. 6.9. Cartesian transformation grids illustrating the shape changes during growth of both populations (PC I score -0.12 to $+0.12$ from the analysis of adult and subadult data after generalised Procrustes registration). Frontal view, A; lateral view, B. Note the relative lateral expansion of the zygomatic region and the relative vertical and horizontal expansion of the maxilla during growth.

also expanded horizontally along the alveolar part of the maxilla, indicating that a feature of growth is relative lengthening of the tooth-bearing part of the maxilla. This is confirmed by more pronounced similar deformations observed in the region of the maxillary alveolus in more medially sited grids (not drawn because of space limitations). This maxillary alveolar expansion accommodates the dentition and results in a moderate increase in maxillary prognathism and greater relative posterior positioning of the posterior limit of the maxilla.

A wireframe model delimiting the principal bones of the face is drawn in Fig. 6.10. Figure 6.10a represents the 'small' or 'young' reference (PC I score -0.12) and 9.10b, the 'large' or 'old' target (PC I score $+0.12$). The principal difference between these figures is that the face of the older individuals is relatively much larger than the younger. This can be seen to be due, in the main, to relative maxillary expansion in all directions, resulting in more lateral siting of an expanded zygomatic. The zygomaticomaxillary suture is relatively increased in length during growth. The palate is increased and the orbit and frontal are decreased in relative size.

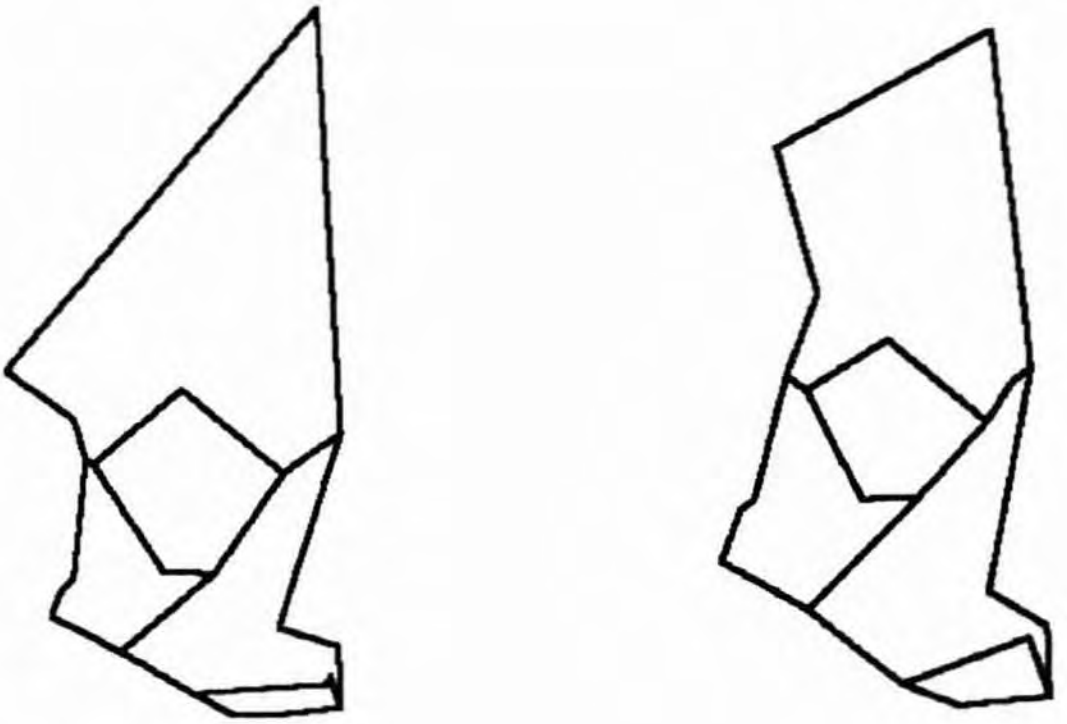


Fig. 6.10. Proportional changes in the skeletal elements of the face during growth illustrated by wireframe model approximately delimiting bone boundaries. (a) Shape represented by score of − 0.12 on PC I; (b) shape represented by score of + 0.12 on PC I.

These analyses lead us to conclude that there is no evidence of different growth allometries between the Alaskans and Aleutians; we have failed to falsify our hypothesis, H2. This common allometry might be extended (hypermorphosis) in Aleutians but our statistical findings are equivocal so we set this possibility aside. In the main, allometric growth in both populations features a relative lateral, vertical and horizontal expansion of the face, especially of the maxilla. The result is that the frontal and orbital regions show a relative decrease in size.

The findings indicate that the principal distinctions in facial morphology between Alaskans and Aleutians are present very early and probably at birth. In our PCA we therefore expect to be able to differentiate Alaskans and Aleutians irrespective of age. Since the first PC represents an allometric growth vector we expect these differences to be present on higher-order PCs (PC II and above).

PC II is plotted against PC I in Fig. 6.6 where it separates Alaskans from Aleutians to some degree. The small-rendered reconstructions drawn at the limits of PC II indicate the transformed mean at the extremes of this component. They show differences that are small in comparison to those on PC I. This finding is consistent with the eigenvalue for PC II, which

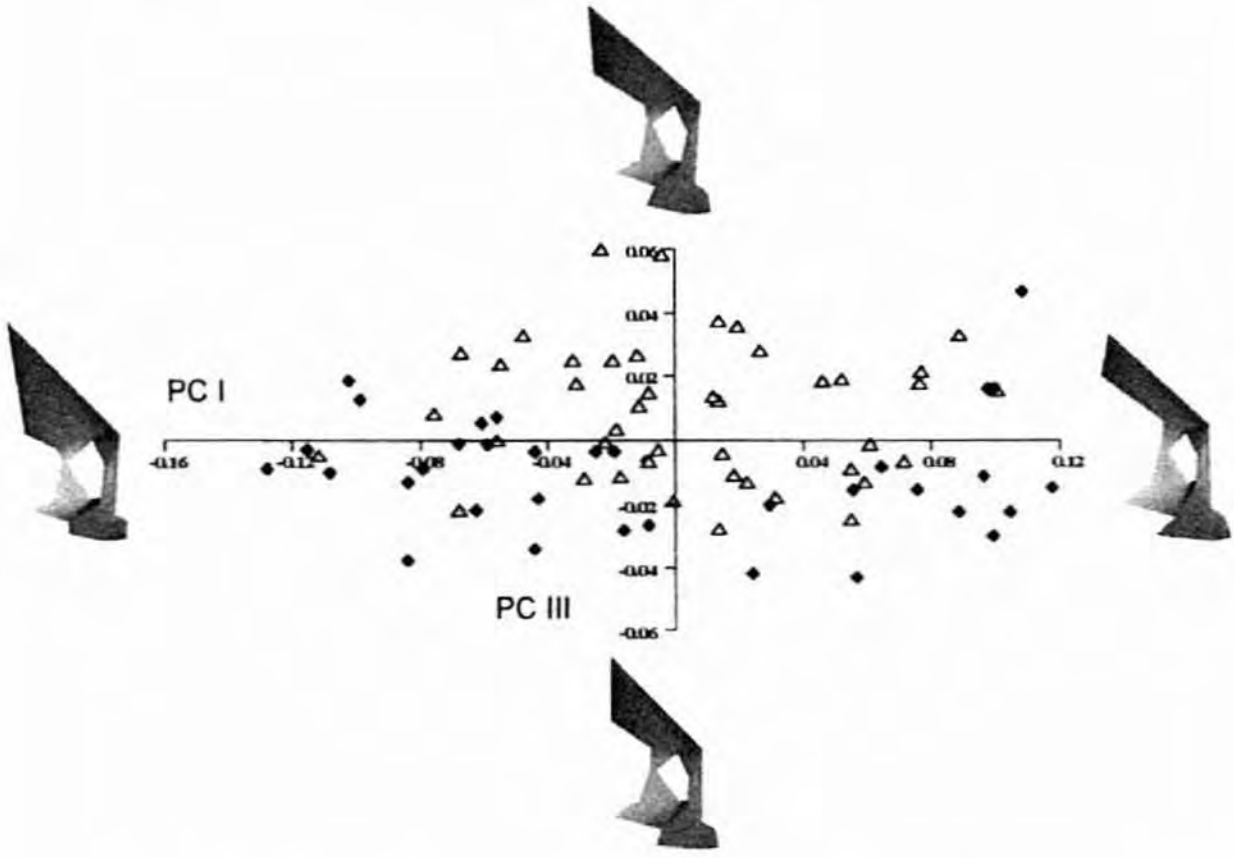


Fig. 6.11. Principal components analysis of adult and subadult data after generalised Procrustes registration. PC I (horizontal axis) vs. PC III (vertical axis). Triangles, Alaskans; diamonds, Aleutians. Small inset figures illustrate shapes represented by scores of $\pm$ 0.12 on PC I and $\pm$ 0.05 on PC III; 5.8% total variance.

indicates that it accounts for only 6.2% of the total variance while PC I accounts for 47.5%. PC II also contrasts with PC I in partially differentiating Alaskans (low scores) from Aleutians (large scores). This differentiation is, however, incomplete in that populations overlap.

Further differences between Alaskans and Aleutians are represented by PC III (Fig. 6.11). The transformed means reconstructed at the extremes of this axis again indicate that differences on this PC are small relative to those occurring during growth. This is consistent with the relative values of the eigenvectors for these components: PC III 5.8% of total variation, PC I 47.5%. PC III, like PC II offers some separation, with overlap, between Alaskans (high scores) and Aleutians (low scores).

No other PC shows clear evidence of separating Alaskans and Aleutians. The contrast between populations is clear when PCs II and III are plotted (Fig. 6.12). Triangles representing Alaskans occupy the upper left of this diagram while diamonds representing Aleutians occupy the lower right, and there is little overlap. The one exception is the Alaskan at PC II $\approx$ 0.035 PC III $\approx$ 0.005, which sits squarely with Aleutians. This is probably explained by distortions in this very young, fragile, specimen. The

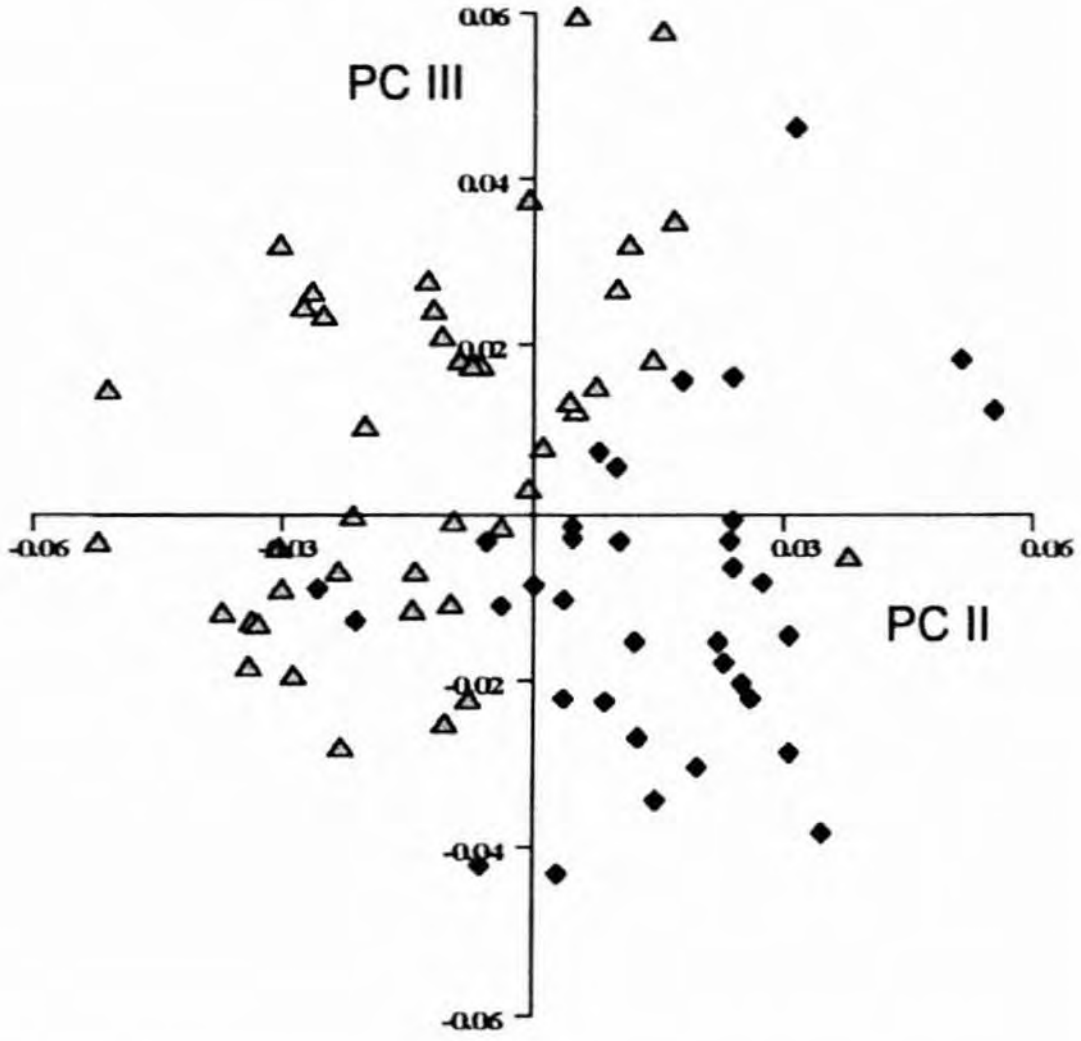
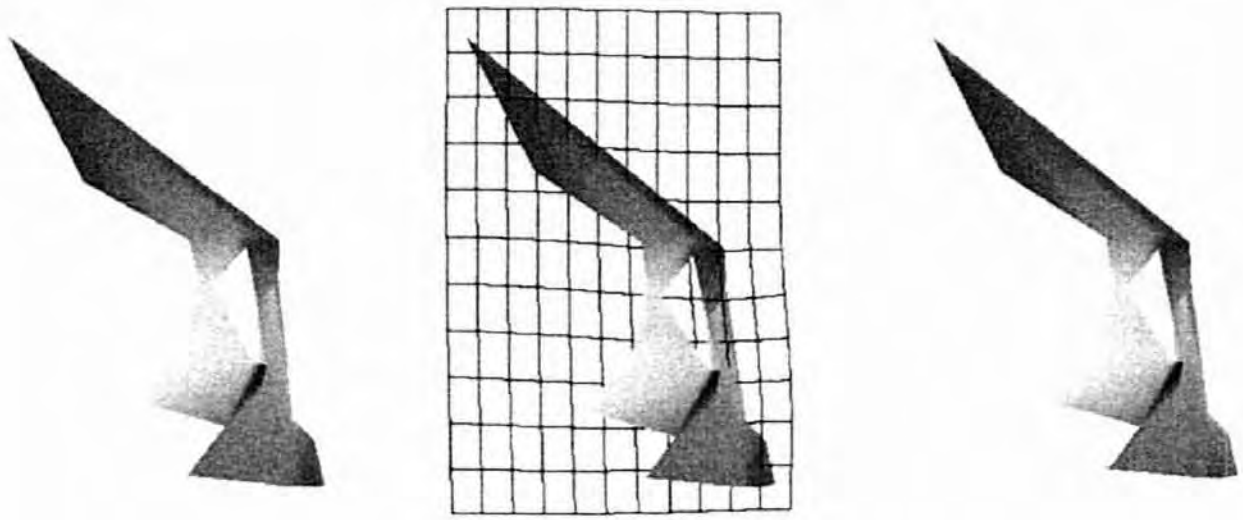


Fig. 6.12. Principal components analysis of adult and subadult data after generalised Procrustes registration. PC II (horizontal axis) vs. PC III (vertical axis). Triangles, Alaskans; diamonds, Aleutians.

differences evident between the populations on PCs II and III are independent of the growth allometry modelled by PC I.

The plot of PCs II and III is reminiscent of that of the first two PCs from the analysis of adults (Fig. 6.4) except that scores of specimens are reflected with respect to the horizontal axis. In both, Alaskans and Aleutians occupy opposite semicircles of the scatter and are nearly completely separated. It is of interest, therefore, to compare this age-independent difference in facial shape with the difference found between adults in the earlier analysis. In Fig. 6.13 the difference at all ages is visualised by comparing rendered transformed means. That in Fig. 6.13a represents the mean Alaskan on PCs II and III and that in Fig. 6.13c, the mean Aleutian. In Fig. 6.13b a transformation grid between these two reconstructions is drawn in a plane which just passes to the right of the midline, since it is in this plane and in this region that the differences are greatest in magnitude. This grid is



A B C

Fig. 6.13. Differences between Alaskan and Aleutians on PCs II and III in the principal components analysis of adult and subadult data after generalised Procrustes registration. (a) Representation of mean Alaskan on PCs II and III; (b) Mean Aleutian on PCs II and III; (c) Cartesian transformation grid illustrating the difference between Alaskan (reference) and Aleutian (target) means on PCs II and III. The deformation between Alaskan and Aleutian is emphasised for the purposes of drawing the grid by multiplying the transformation by a factor of 2.

multiplied by a factor of 2 to aid interpretation. It indicates that the age-independent difference between Alaskans and Aleutians is small but consists in the main of a greater anterior projection of the midface and nasal region in Aleutians with respect to Alaskans. The transformation grid showed little distortion in the coronal and transverse planes.

Figure 6.13 is very similar to Fig. 6.5, in which adult means alone are compared. The differences between adult population means are very similar to the age-independent difference found between populations at all ages. The degree of difference between adults is, however, greater and the difference includes some relative upward bending of the grid to the bottom left (Fig. 6.5b vs. Fig. 6.13b). This is probably explained by the omission of small differences represented by PCs IV–LXXI in the reproduction of Fig. 6.13b. The overwhelming similarity between Fig. 6.5b and 6.13b, together with the similarities found in all other planes examined, lead us to conclude that the differences in shape found between adults are largely present postnatally and are continued into adulthood.

Thus Alaskans and Aleutians share a common growth allometry that serves to preserve into adulthood differences in facial morphology present at birth. This finding contrasts with the differences found amongst other populations in as yet unpublished studies being undertaken by one of us

(U.S.V.). It should not be assumed, therefore, that differences in facial morphology between modern human populations are generally fully expressed at birth or that all modern populations share the same facial growth allometry. It will be of interest in future analyses to examine the extent to which differences in growth allometries might be related to population divergence.

Discussion

The study of the ontogeny of facial form we present in this chapter has served to demonstrate the potential of the techniques of geometric morphometrics in the study of three-dimensional growth changes. These methods result in highly visual representations of shape differences and allometric growth models. Additionally conventional statistical analyses are possible in the tangent space.

Our findings are, first, that the adult crania of Alaskans and Aleutians differ in morphology; H1 is falsified. Secondly, that the populations share a common facial growth allometry; H2 is falsified. This leads to the third finding that a substantial part of the differences in shape present between adults can be observed between even the youngest individuals.

Differences in midfacial prognathism and nasal projection are present by the end of the first postnatal year (we have no earlier data) and are continued into adulthood. Growth contributes little to further accentuation of these differences. Our data suggest that Aleutians extend the common growth allometry relative to Alaskans but this finding just fails to achieve statistical significance. More data are needed to confirm or deny this.

It seems likely that the influences on postnatal facial growth (see Introduction) are identical between these closely related populations. However, before the first postnatal year, a fundamental difference in facial morphology is established. The nature of this difference is such that it does not modify subsequent growth allometry between populations and this implies that growth trajectories are to some degree independent of, or can compensate for, initial form. The limits of this independence between growth allometry and form at the end of the first postnatal year need to be explored through growth studies of more divergent populations and different species. The findings of such studies will cast further light on the mechanisms regulating growth allometry.

The finding of a difference in facial morphology between these populations that is independent of age opens up the possibility of generating an

age-independent discriminant function to enable forensic identification of subadult material. This is an interesting finding that we intend to pursue with respect to other human populations, since the practical application to forensics is of great potential value.

This example study has served to indicate how facial growth might be readily compared using tools from the geometric morphometric toolkit. These tools are relatively new and advances in statistical understanding and computer graphics will inevitably open up exciting new possibilities in the future. An important new horizon lies in combining these tools with modern imaging modalities in order to allow analysis of images from computed tomography (CT) (Spoor and Zonneveld 1995; Spoor 1997) and magnetic resonance imaging (MRI). It should be soon possible to undertake, with reasonable effort, studies where internal morphology as well as external contributes to models of growth and where the three-dimensional visualisations and animations are of the level of quality we have come to expect from modern CT and MRI.

In particular, the methods we have outlined here offer considerable potential in understanding the ontogenetic basis of morphological variation and its relationship to evolutionary adaptation and divergence. Insights into the means by which modern taxa become different through growth might well prove of value in the interpretation of evolutionary divergence. Future studies will indicate the extent to which such growth variations are useful in understanding adaptation and phylogeny. Thus, interpretation of the significance of growth variations in the past depends to a great degree on knowledge of variations in the present.

These technologies are, of course, applicable in studies of the morphology of any anatomical region. In applying such technologies, however, it is important that a keen eye is kept on the biological issues at hand. It is easy to fall into the trap of producing visually appealing analyses devoid of biological hypothesis testing simply because the technology is there. The difficulty for anthropologists of the future will lie not in technical issues of analysis but rather in devising testable hypotheses of biological merit.

Acknowledgements

This work is entirely dependent on the considerable programming efforts of Nicholas Jones, who made it possible to carry out the analyses and generate images in a relatively straightforward way. Professor Christoper Stringer of the Natural History Museum, London, has been pivotal in enabling and supporting U.S.V. in these studies. The programming and the

studies described in this chapter could not have been undertaken without the support of our statistical colleagues – Professor Kanti Mardia, Dr Ian Dryden and Professor John Kent of the Department of Statistics, University of Leeds. Others have also contributed valuable advice. These include Dr Fred Bookstein (Michigan), Dr Les Marcus (New York) Professor Jim Rohlf (New York) and Dr Subhash Lele. Professor Christoper Dean and Dr Fred Spoor have been supportive and stimulating in discussions leading to this work.

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